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Seasonal variation in the relative dominance of herbivore guilds in an African savanna

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Abstract

African savannas are highly seasonal with a diverse array of both mammalian and invertebrate herbivores, yet herbivory studies have focused almost exclusively on mammals. We conducted a two-year exclosure experiment in South Africa's Kruger National Park to measure the relative impact

of these two groups of herbivores on grass removal at both highly productive patches (termite mounds) and in the less productive savanna matrix. Invertebrate and mammalian herbivory was greater on termite mounds, but the relative importance of each group changed over time. Mammalian offtake was higher than invertebrates in the dry season, but can be eclipsed by invertebrates during the wet season when this group is more active. Our results demonstrate that invertebrates play a substantial role in savanna herbivory and should not be disregarded in attempts to understand the impacts of herbivory on ecosystems.

Keywords: exclosure experiments, grasshoppers, insect herbivory, Kruger National Park, *Macrotermes*, nutrients

Introduction

Herbivory is an important process in ecosystems across the globe, and, together with fire, is largely responsible for limiting the structure and composition of plant communities over large parts of the terrestrial surface (Bond 2005, Hempson et al. 2015). Herbivory alters the stability of ecosystems through indirect effects on the balance of vegetation types (e.g., trees and grass in savannas, van Langevelde et al. 2003), modifies vegetation structure through direct consumption (Asner et al. 2009), and affects plant and animal abundance and diversity (Olff and Ritchie 1998, Pringle et al. 2007). However, studies examining herbivory and its effects on ecosystems have largely focused on single herbivore functional groups (i.e. either large mammals or insects), with few studies comparing the relative roles of each group (Risch et al. 2015). Moreover, most studies investigating the effects of herbivores in African savannas have focused on large mammals, with far more numerous, albeit smaller in size, invertebrate herbivores largely ignored in calculations of herbivory and consumer control of savanna ecosystems. This despite the fundamental functions performed by invertebrates and the substantial contribution they likely make to herbivory, even outweighing that of vertebrates in some systems (La Pierre et al. 2015). Therefore, the role of invertebrate herbivory in the

consumer control of ecosystems, and how it compares to vertebrates, warrants further attention (Andersen and Lonsdale 1990, Risch et al. 2015).

Herbivory is not a static process, but varies across landscapes in response to productivity gradients and foliar nutrition, with mobile herbivores adjusting their foraging activities to avoid predators and/or unfavorable forage (Pitt 1999, Anderson et al. 2010, Ford et al. 2014). As such, some areas experience higher levels of herbivory than others, with the resulting effects of herbivory varying across space. Furthermore, seasonal differences in many parts of the world cause many herbivores to migrate or become seasonally dormant, resulting in temporal variation in herbivory effects (Frank et al. 1998, Jonzén et al. 2002). Invertebrates, in particular, display strong responses to seasonality, often more so than vertebrates, including migratory and/or diapause behavior in response to adverse seasonal conditions (Wolda 1988). Their relative contribution to herbivory compared to vertebrates might therefore be expected to vary temporally.

Savannas are highly variable environments that experience dramatic differences in productivity and foliar nutrition over multiple spatial scales ranging from landscapes to small scaled shifts in soil fertility over tens of meters (du Toit et al. 2003). Herbivores respond to this variation by altering their foraging activities to maximize energy intake, with their effects on vegetation being equally dramatic over similar spatial scales (Olff and Ritchie 1998, Asner et al. 2009). Landscape features that differ from their broader surroundings in terms of increased productivity or fertility often act as foraging hotspots in savannas and can play important roles in mediating herbivore distributions and effects. Termite mounds are one such feature, where, through termite activity (the concentration of soil nutrients, organic material and moisture), mound soils become nutrient-enriched and support compositionally distinct, nutrient-rich plant communities (Sileshi et al. 2010, Jouquet et al. 2011). These vegetation communities result in termite mounds becoming foraging hotspots, favored by a diverse range of browsing and grazing mammals (Mobæk et al. 2005, Levick et al. 2010, Davies et al. 2015). Termite mounds are also known to harbor a greater abundance of insects than corresponding adjacent areas (Pringle et al. 2010, Leitner et al. *in prep*), and are likely

important features for invertebrate herbivores. Yet, despite the large biomass and diversity of invertebrates in savanna systems (Gandar 1982, Braack and Kryger 2003), previous research has largely ignored invertebrate herbivory, both at highly productive sites (such as termite mounds) and in the background savanna matrix. Instead, large mammalian herbivores receive the majority of attention in savanna herbivory work, particularly in Africa where many charismatic, mammalian megaherbivore species persist.

Here, we made use of a two-year exclusion experiment to measure the relative contribution of large mammals and invertebrates to savanna grass herbivory, including how their relative influence varies across seasons. Furthermore, we compared levels of herbivory on termite mounds built by *Macrotermes* (high quality forage) to those in the savanna matrix (lower quality forage), examining the importance of such high productivity patches for both groups of herbivores. We expected both mammalian and invertebrate herbivory to be greater on termite mounds than in the savanna matrix, but predicted that the relative importance of vertebrate and invertebrate herbivores would differ between seasons, with greater herbivory by invertebrates during the wet season when they are active and abundant, and relatively higher levels of mammalian herbivory in the dry season because mammals remain active throughout the year.

Methods

Study site

We conducted the experiment in a semi-arid savanna system (mean rainfall ~ 625 mm.yr^{-1}) in southern Kruger National Park (KNP), South Africa. The tree layer here is dominated by *Combretum zeyheri* and *C. collinum*, dominant grass species on termite mounds are *Panicum maximum* and *Urochloa mosambicensis*, whereas in the savanna matrix *Digitaria eriantha*, *Eragrostis rigidior* and *Pogonarthria squarrosa* are common (Davies et al. 2014b). The topography consists of an undulating landscape on granitic substrate; *Macrotermes* mounds occur predominantly on sandy, relatively nutrient-poor crests and upper sections of hillslopes (Davies et al. 2014a). Primary mammalian

grazers and mixed-feeders in the study area include white rhinoceros (*Ceratotherium simum*), Cape buffalo (*Syncerus caffer*), plains zebra (*Equus quagga burchellii*), blue wildebeest (*Connochaetes taurinus*), impala (*Aepyceros melampus*), elephant (*Loxondonta africana*) and waterbuck (*Kobus elipsiprimnus*). An abundant and diverse invertebrate fauna is present in the region (Braack and Kryger 2003), with invertebrate herbivory in savannas likely dominated by grasshoppers (Sinclair 1975, van der Plas and Olff 2014).

Experimental design

Ten termite mounds, located on crests and spaced at least 50 m (and in most cases over 100 m) apart, were selected for the experiment. All surveyed mounds were built by the genus *Macrotermes*, with the dominant species in the area being *M. falciger* and *M. natalensis* (Davies et al. 2014a). Two types of exclosures (full and partial) measuring a cubic meter were constructed and deployed in January 2012, using a modification of the movable cage method (McNaughton et al. 1996). The full exclosures consisted of a 200 x 200 mm metal grid covered with 2 x 2 mm aluminum gauze mesh, pegged at ground level and designed to exclude mammalian and invertebrate herbivores, whereas the partial exclosure consisted only of the metal grid to exclude large mammalian herbivores, but allow access by invertebrates. Invertebrates were manually removed during construction of the full exclosures and the metal grids were small enough (~200 x 200 mm) to prevent mammalian herbivores accessing vegetation within the exclosures. Measurements were recorded from the center of the exclosures to reduce the possibility of any potential herbivory at the edges. A control site was established one meter adjacent to each exclosure. The design was set-up on the pediment of the ten termite mounds, with paired sites (exclosures and control) established 30 m into the savanna matrix, in a random direction from each corresponding mound. The exclosures were maintained for two years (January 2012 – February 2014), including a full repair in November 2012 following a natural fire. Although fire is a common occurrence in savanna ecosystems and known to affect herbivore foraging and distributions (Archibald and Bond 2004), effects of single fire events on

herbaceous vegetation cover do not last longer than a few months, following which vegetation regrows and structural differences disappear (Parr, et al. 2004, Radford and Andersen 2012).

Thermochron iButtons® (Maxim/Dallas Semiconductor Corp., USA) recording temperature and relative humidity were placed approximately 2 cm below the soil surface in eight paired exclosures (four full and four partial) to record any potential alterations in micro-climate caused by the mesh of the full exclosure. iButtons were placed in January 2012 and removed in June 2012. At approximately bimonthly intervals beginning in January 2012, grass biomass readings were recorded in each exclosure and control site using a disc pasture meter. The disc pasture meter has been calibrated for this vegetation type and standing biomass was calculated with the following formula from Trollope (1990):

$(\sqrt{X} \times 2260) - 3019 = \text{kg ha}^{-1}$

where X is the disc height reading in cm obtained from the disc pasture meter.

Data analysis

All statistical procedures were conducted using R software version 2.15.1 (R Development Core Team 2012). A candidate set of 13 generalized linear mixed-effects models with Poisson error distributions was constructed to examine relationships between standing grass biomass (dependent variable) and herbivore exclusion (full or partial exclosure and control plots), season (wet and dry), location (on termite mounds or in the savanna matrix) and the two-way interactions between treatment (level of herbivore exclusion) and season and treatment and location (Table 1). Termite mound identity was considered a random effect. Grass biomass was rescaled by multiplying it by 10^{-2}. Data from September and November 2012 were excluded from analysis because of the fire. Models were applied using the *lme4* package in R (Bates et al. 2007) and ranked according to sample-size-corrected AIC*c* (Burnham and Anderson 2002) using the R package *MuMIn* (Barton 2010), with the most parsimonious model for each response variable selected for further analysis (Table 1). Effects of each fixed effect present in the top model were examined using Type III

likelihood-ratio Chi square tests with the R package *car* (Fox et al. 2012). After application of the top model, multiple comparisons of means *post-hoc* testing for mixed-effects models, using Tukey contrasts averaged across interaction terms, was used to examine pairwise comparisons with the R packages *multcomp* (Hothorn et al. 2008) and *mvtnorm* (Genz et al. 2011).

Actual grass biomass removed by invertebrate and mammalian herbivores on termite mounds and in the savanna matrix was calculated from the mean standing biomass measured in the exclosures. Total consumption (combined invertebrate and mammalian consumption) was calculated as the difference in standing biomass between the full exclosures and the control plots. Invertebrate consumption was calculated as the difference between the full and partial exclosures and mammalian offtake as the difference in standing biomass between partial exclosures and controls.

Results

Neither temperature nor relative humidity differed between full and partial exclosures (temperature: Paired Wilcoxon Rank Sum Test, W = 1, p = 0.25, n = 4; humidity: W = 4, p = 0.88, n = 4). Microclimatic conditions were therefore considered similar between exclusion treatments.

Treatment (exclosure type, X^2 = 1574.406, p < 0.001), season (X^2 = 146.727, p < 0.001) and location (on or off termite mounds, X^2 = 487.579, p < 0.001) had a significant effect on standing grass biomass. The interactions between treatment and season (X^2 = 46.008, p < 0.001) and treatment and location (X^2 = 832.279, p < 0.001) also had a significant effect on biomass. The dry season had significantly lower standing biomass than the wet season (p < 0.001), with seasonal differences most pronounced at the termite mound control sites, where grass biomass was depleted during the dry season, but generally maintained in the exclosures and savanna matrix (Fig. 1). Biomass inside full (excluding mammalian and invertebrate herbivores) and partial (excluding mammalian herbivores) exclosures was significantly greater than the controls (p < 0.001 for both mounds and matrix), and was significantly higher (p < 0.001) in full exclosures compared to partial ones, at both mounds and

in the matrix, with greater differences recorded during the wet season (Fig. 1). Standing biomass was also significantly greater at the matrix control sites than the mound controls ($p < 0.001$), whereas biomass at partial and full mound exclosures was significantly higher ($p < 0.001$) than the paired treatments in the savanna matrix. When comparing control plots with exclosures, the magnitude of difference (effect size) between treatment and control was much greater on mounds than in the matrix (Fig. 1).

Herbivory was greatest on termite mounds for both consumers (Fig. 1), and the relative contributions of each consumer varied with season (Fig. 2). On termite mounds, mammalian herbivores removed more grass biomass relative to invertebrate herbivores during most of the experiment; however, invertebrates removed substantially more biomass during the wet season, exceeding mammalian offtake during the second wet season (Fig. 2a). Herbivory in the matrix was substantially lower than on mounds, with mammalian offtake exceeding that of invertebrates for all time periods apart from the second wet season when invertebrate herbivory was substantially greater than that of mammals (Fig. 2b).

Discussion

Our results provide strong evidence that invertebrate herbivores are a significant group in savannas and warrant greater attention. Despite their diversity and abundance, invertebrates generally receive less attention compared to vertebrates in savanna research (Braack and Kryger 2003), with only a handful of studies on invertebrate herbivory (e.g. Sinclair 1975, Gandar 1982, Andersen and Lonsdale 1990). However, our findings demonstrate that the importance of these herbivores should not be underestimated, with their contribution to savanna grass offtake being comparable to, and sometimes exceeding, that of mammals.

The contribution of invertebrate herbivory to grass removal surpassed mammalian offtake during the second wet season and likely reflects greater invertebrate activity during the wetter months (Sinclair 1975, Braack and Kryger 2003). When invertebrate activity decreases during the dry

season, mammalian herbivores become relatively more important, consuming more grass biomass at both termite mounds and in the savanna matrix. Therefore, herbivory by both invertebrates and mammals is important in savanna ecology, but the dominance of their respective roles is temporally variable. In migratory systems where mammalian herbivores migrate each year in response to unfavorable seasonal conditions, and where invertebrates are also inactive during such times, herbivory will be highly seasonal and the relative roles of each group will likely not differ throughout the year, as is the case in the short grass plains of the Serengeti (Sinclair 1975). However, in seasonal systems with sedentary mammal populations, such as our study site, overall herbivory will increase substantially in the wet season as invertebrates become active and contribute to on-going mammalian herbivory, as is the case in the Serengeti long grassland systems (Sinclair 1975) and the matrix sites in our study (Fig. 1b). Although invertebrate herbivory did not eclipse that of mammals during the first wet season, it did increase in a similar fashion to the second wet season on termite mounds. Invertebrate herbivory in the first wet season might have been reduced due to the extensive fire a few months prior that could have temporarily reduced population sizes of some invertebrates (see Swengel 2001 for a review of insect responses to fire). Furthermore, mammalian herbivores respond to post-fire vegetation regrowth and are attracted to recently burnt areas, leading to higher mammalian grazing pressure in these areas (Archibald and Bond 2004). In contrast, most invertebrate herbivores are likely unable to exhibit as much flexibility in their movements and spatial distributions due to their smaller body size and subsequent inability to travel large distances.

The greater invertebrate herbivory recorded on termite mounds compared to the savanna matrix indicates that invertebrates preferentially feed on mound vegetation in similar ways to mammals (Fig. 1). Indeed, Leitner et al., (*in prep.*) recorded higher grasshopper (likely the dominant invertebrate herbivore) abundance on mounds than in the matrix at the same study sites, likely driving patterns of increased invertebrate use of mound vegetation. Similarly, Pringle et al., (2010) recorded higher abundance of herbivorous insects on termite mounds in east Africa. A wide range of ungulate species (e.g. from warthog to white rhino) are known to preferentially graze on termite

mounds (Mobæk et al. 2005, Cromsigt and te Beest 2014), and our results indicate that such general preferences also extend to invertebrates. Termite mounds have been shown to support significantly different grass assemblages (Jouquet et al. 2004, Moe et al. 2009), which are also higher in nutritional content (Grant and Scholes 2006, Davies et al. 2014b) than the surrounding matrix, including higher levels of N and P, essential nutrients for both mammalian (Owen-Smith and Novellie 1982, Grant and Scholes 2006) and invertebrate herbivores (Lewis 1984, Stiling et al. 1999). It is therefore not surprising that they are heavily used by both groups of grazers. Other factors, such as predation risk, are also important drivers of herbivore foraging decisions (Pitt 1999, Anderson et al. 2010). However, given the relatively small size of the nutrient enriched vegetation patches on and around termite mounds, possible attraction based on anti-predator benefits (e.g., raised terrain and open vegetation around mounds leading to potentially improved visibility for herbivores) is unlikely for mammalian herbivores. Similarly, termite mounds are unlikely to provide anti-predator advantages to invertebrates, but could instead be risky habitats because predatory invertebrates, such as spiders, also occur in higher numbers around mounds, probably because of increased prey availability (Pringle et al. 2010).

The lower herbivore pressure in the savanna matrix by both mammals and invertebrates results in smaller absolute differences in herbivory between these groups here, with larger differences evident under heavy grazing pressure at productive sites (termite mounds). Nevertheless, the same patterns are evident in the matrix as on termite mounds, demonstrating that although differences between invertebrate and mammalian herbivory are greater on mounds, the relative roles of each group (including seasonal differences) persist through a range of ecological conditions, such as varying productivity. Further testing of the relative roles of these two herbivore groups in variable environmental conditions will improve our understanding of both the persistence of our recorded patterns, as well as whether termite mounds are always favored by both groups (see Davies et al. 2015). Moreover, comparisons between invertebrate and mammalian herbivory will need to be made in systems with both higher and lower mammal and invertebrate abundance

before a full understanding of their relative contributions is achieved. In places where mammalian biomass is very high (e.g. the Serengeti), invertebrates might be expected to play a smaller role (Sinclair 1975). Conversely, invertebrate herbivory will likely be more important in systems largely devoid of sizeable mammal populations. Such differences in the type of dominant herbivory could lead to differences in the composition of plant communities as a result of differing preferences for plant traits and co-evolved plant-herbivore interactions. Furthermore, shifts in the dominant herbivore group, e.g. due to invasions or population declines, could lead to changing plant communities (Tanentzap et al. 2010).

The increased mammalian herbivory at termite mounds during the dry season, compared to relatively constant levels throughout the year in the savanna matrix, is indicative of termite mound vegetation being more heavily used by mammalian herbivores during the dry season when savanna matrix grasses lose nutritional value and herbivores rely more on nutrient-rich mound grasses (Davies et al. 2015). Some of this dry season increase in measured herbivory could be attributed to the lack of regrowth during this season, however, the main aim of our study, to understand how invertebrate herbivory compares to mammalian herbivory, is not compromised because the vegetation in the invertebrate exclosures would similarly not regrow in the dry season. Regrowth during the wet season suggests that our measured offtake in this season is an underestimate, and actual offtake is likely higher since much of the vegetation removed during the two months between measurements will have regrown.

Herbivory is an important process in ecosystems around the world, affecting ecosystem functioning, species composition and vegetation structure (Olff and Ritchie 1998, Pringle et al. 2007, Asner et al. 2009), but efforts aimed at understanding its effects will be insufficient if they focus only on large mammalian herbivores. Invertebrates, as well as other groups such as small mammals (Keesing 2000), need to be considered for the full picture to emerge. This is particularly true for African savannas where much attention has focused on the charismatic mammalian fauna, despite a diverse and abundant invertebrate fauna. Moreover, many parts of the globe have suffered

mammalian extinctions (Ripple et al. 2015), but invertebrate communities are relatively intact, and can therefore be expected have a wider ranging impact, including in human dominated and agricultural landscapes. We would do well to consider them in attempts to understand the importance of herbivory in ecosystems.

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Table 1: The set of regression models applied to relationships between standing grass biomass on termite mounds and in the savanna matrix in full and partial herbivore exclosures and control sites. Models are ranked according to the second order Akaike Information Criterion (AICc). The most parsimonious model, used in the final analysis, is in bold. w_i is the Akaike weight of the model. For all models, termite mound identity was a random effect.

Rank	Form of regression model	AIC_c	No. parameters	ΔAIC_c	w_i
1	**Treatment + Season + Location + Treatment*Season + Treatment*Location**	**7519.7**	**6**	**0.00**	**1.00**
2	Treatment + Season + Location + Treatment*Location	7561.8	5	42.09	0.00
3	Treatment + Location + Treatment*Location	7793.0	4	273.24	0.00
4	Treatment + Season + Location + Treatment*Season	8385.8	5	866.05	0.00
5	Treatment + Season + Treatment*Season	8400.3	4	880.62	0.00
6	Treatment + Season + Location	8429.1	4	909.42	0.00
7	Treatment + Season	8443.4	3	923.74	0.00
8	Season + Location	8662.0	3	1142.29	0.00
9	Treatment	8676.0	2	1156.30	0.00
10	Season + Location	11188.8	3	3669.10	0.00
11	Season	11209.0	2	3689.29	0.00
12	Location	11349.3	2	3829.59	0.00
13	Intercept	11369.0	2	3849.34	0.00

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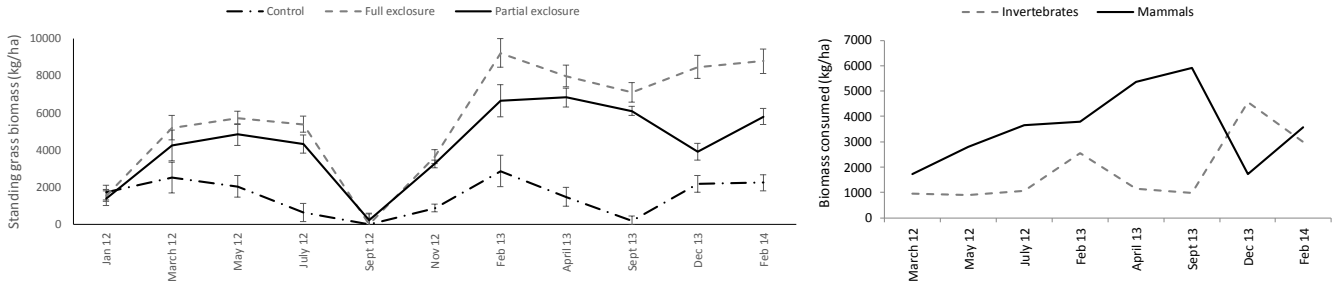
Figure 1: Left-side panels: standing biomass (kg.ha^{-1}) of grass in full herbivore exclosures (excluding both large mammals and invertebrates), partial exclosures (excluding mammals only) and control sites at a) termite mounds and b) savanna matrix plots at Napi, Kruger National Park. The low biomass measurements recorded in September 2012 were due to a natural fire and were excluded from analyses, as were November 2012 measurements when exclosures were re-constructed. Right-side panels: biomass removal (calculated from the mean biomass measured in the full and partial exclosures and control plots) by each herbivore guild (large mammals and invertebrates) at a) termite mounds and b) savanna matrix plots. The period July 2012 to February 2013 was excluded from analysis due to the fire.

Figure 2: The relative contribution (proportion) of grass biomass removed by insect and mammalian herbivores at a) termite mounds and b) savanna matrix sites at Napi, Kruger National Park. Removal was calculated from the mean biomass measured in the full and partial exclosures and control plots. Data were not collected between July 2012 and February 2013 due to a natural fire that consumed all grass biomass. The dry season is considered to last from late April/May until September.

Figure 1
a)



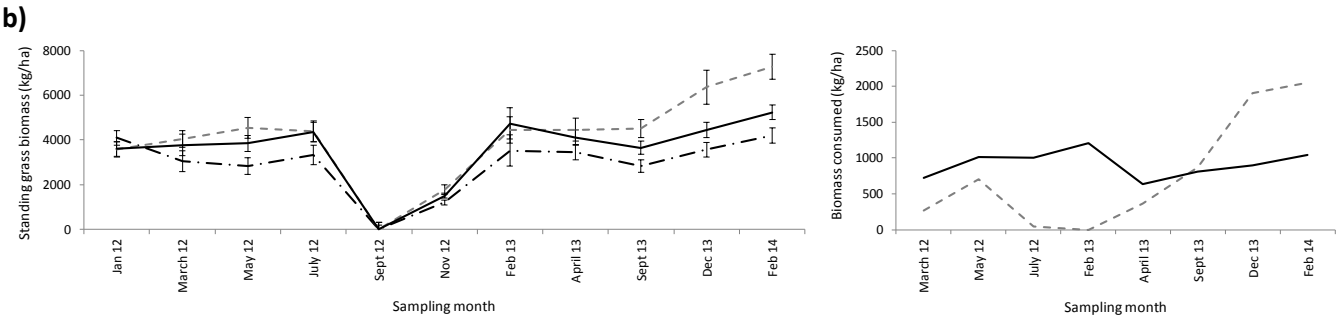


Figure 2